

## NEW COMBINATIONS AND TAXA OF HEPATICAE, I.

Rudolf M. Schuster  
Cryptogamic Laboratory  
Hadley, Massachusetts<sup>1</sup>

Two major, continuing projects have occupied my attention for over 30 years, The Hepaticae and Anthocerotae of North America [Columbia University Press, Vol. I (1966), II (1969), III (1974), IV (1980; in press)] and "The Hepaticae" for Die Natürlichen Pflanzenfamilien, ed. II. The long time span necessary for completion of these works poses special problems. Thus, in Schuster (1966, pp. 381-86) a new classification of Hepaticae is offered -- with several new taxa proposed. At present (February, 1980), those taxa pertaining to Vols. IV and V of my Columbia University series remain, technically, nomina nuda. However, several have been validated and appear as "Schust. ex" in the works of others. Other taxa proposed have been published, simultaneously, or earlier or later, by other workers. Thus, on p. 382 (Schuster, 1966) the subf. Mytilopsidoideae of the Lepidoziaceae is proposed, technically a synonym of subf. Micropterygioidae Grolle, which appeared slightly earlier. Similarly, on p. 382 the name "Haplochaete Schust." appears which was to be validated in the same volume (p. 724) under the Blepharostomataceae. Between the time corrected page proofs including p. 382 were returned, and the time the signature including p. 724 was returned, a paper by Hodgson appeared describing the same entity as Isophyllaria. Footnote 22, p. 724, was abbreviated and emended, and "Isophyllaria Hodgs." was substituted for "Haplochaete Schust." On p. 385, under the Pelliaceae, subfamilies Verdoornioideae and Allisonioideae are cited as new groups; I intended to discuss and validate these in Vol. IV of this series -- but they appear in Grolle (1972) as "Allisonioideae Schust. subf. n." [to be cited as "ex Grolle"] and in Inoue (1976) as "Verdoorniaceae Inoue" and Allisoniaceae (Schust.) Schust. et Inoue. Other cases could be cited, but I think my point has been made. Long-continued delays in validation of names pose problems both for my work and for that of others. It results in confusion and in duplication of names.

The pragmatic alternative is to validate the names, making new combinations and adjustments in rank where needed, prior to any meaningful discussion of the entities. I have consciously refrained from rushing into print with new names and combinations -- and have seen literally dozens of combinations made in manuscript appear elsewhere. Thus, since I first worked up the Cheilolejeunea clausa-trifaria complex for Vol. IV, and inferentially placed "Euosmolejeunea" trifaria into Cheilolejeunea (1955; Jour. Elisha Mitchell Sci. Soc.), the combination of Cheilolejeunea trifaria has appeared elsewhere -- as well as dozens of other combinations under Cheilolejeunea, which I have had in manuscript since 1955.

For this reason, I publish herein the first series of new taxa and combinations and give only enough comment so that my reasoning is clear to my colleagues; detailed justification for the nomenclatural or taxonomic decisions adopted will appear elsewhere, in their proper and meaningful places.

#### Family TRICHOCOLEACEAE

Leiomitra mastigophoroides Schust., sp. n. Trichocoleae simile foliis amphigastrisque quadrifidis ciliatisque necnon cellulis foliorum papillosis et linearibus ad oblongas, necnon ramificatione libere laterali typi Frullaniae; differens ut (a) gynoecea solum in ramis lateralibus brevissimus atque eorum innovationibus reperta, necnon (b) rami ventrali-terminales interdum adsunt. Type. Dominica: Morne Trois Pitons (RMS 66-751).

Possibly the type species will prove identical to Trichocolea flaccida (Spr.) Jack & Steph. [Leiomitra flaccida Spr., Trans. Proc. Bot. Soc. Edinburgh 15:349, 1885] sensu Fulford (1962), but Spruce describes this species as with "♂ in caulis apice incrassato terminalis." The type of Leiomitra, L. tomentosa (Sw.) Lindb. [Hepaticae, in Hibern., p. 515, 1875], is described by Spruce as with the gynoecea "in caule et ramis paucis superioribus terminales, corymbulum sistentes" -- which fails to fit our species. However, he describes a form of this (Cerro Campana, Peru) as with gynoecea "autem semper ramigenis, nunquam in ipso caule terminalibus" -- which fits our species. L. tomentosa is otherwise very different, and L. mastigophoroides clearly keys to Trichocolea flaccida in Fulford (1962).

In any event, the Mastigophora-like, abbreviated lateral branches to which gynoecea are confined (these gynoeceal branches are followed, on the main axis, with "normal, tapering, simple sterile" branches) are highly distinctive. Gynoecea never occur on main axes; those of short lateral branches either lack innovations entirely or sometimes have a highly abbreviated innovation that almost immediately is again gynoeceal; then 2-3 gynoecea may occur, serially, Taxilejeunea-like, on a single, short, lateral branch.

I describe L. mastigophoroides as a new species even though it will almost surely prove identical to one of the synonyms cited under "Trichocolea flaccida" by Fulford (1962): T. patula Steph., T. inaequalis Steph., T. eggersiana Steph., T. herzogii Steph. However, if the synonymy in Fulford is correct, then L. mastigophoroides cannot be identical to any of these plants, since L. flaccida was described by its author as with gynoecea terminating leading axes ("stems"), rarely on branches. The synonymy in Fulford is poorly established and she states that (even though under "examined material" she lists the types of these purported synonyms) she has not seen the "female inflorescence" of T. flaccida. There is much confusion as to the type of at least two of these synonyms: Stephani (Spec. Hep. 4:57, 1909) cites the type of T. patula Steph.

as from Cordillera de Merida [Venezuela], Fulford states "Dominica: s.l. Eggers." Stephani cites the type of T. eggersiana Steph. (Spec. Hep. 4:59, 1909) as from "Santo Domingo," whereas Fulford cites it also as from Dominica: "s.l., Elliott, type of T. eggersiana," and fails to cite the species at all from Santo Domingo! Only with regard to the types of T. inaequalis Steph. (Spec. Hep. 4: 58, 1909) and T. herzogii Steph. (Biblioth. Bot. 27:230, 1916) do Stephani and Fulford agree.

In my opinion, Leiomitra is fully generically distinct from Trichocolea. With the discovery of a, admittedly single, ventral-terminal, Acromastigum-type branch in Leiomitra mastigophoroides, the position of the Trichocoleaceae is again subject to re-investigation. I once (Schuster, 1959) noted that in numerous ways Temnoma (generally placed into the Blepharostomataceae or Pseudolepicoleaceae) is very similar to Trichocolea (placed in the Trichocoleaceae). Indeed, the presence of a free calyptra + short perianth capping the coelocaul in Leiomitra is exactly as shown for Temnoma (Schuster, 1966, 1967). Hence I think that Leiomitra intimately connects the two families to the point where they must be merged. The following synonymy ensues:

Trichocoleaceae Nakai, in Y. Ogura, Ordines, familiae... a Prof. Nakai... edita, p. 200, 1943 [Tokyo].

Blepharostoma[ta]ceae K. Müll., Sv. Bot. Tidskr. 42:14, 1942 [nom. invalid.]

Pseudolepicoleaceae Fulf. & Tayl., Nova Hedw. 1:411, 1960; new syn.

Herzogiariaceae Fulf., Nova Hedw. 1:397, 1960; new synonymy.

Chaetocoleaceae Fulf., Mem. N.Y. Bot. Gard. 11(1):62, 1962; new syn.

Subf. Temnomoideae Schust., Candollea 21:65, 68, 1967 [under Blepharostomataceae].

Subf. Chaetocoleoideae Schust., Candollea 21:65, 1967 [without Latin diagn.]

Subf. Trichocoleoideae

Subf. Blepharostomatoideae Grolle, Jour. Bryol. 7(2):205, 1972 [under Pseudolepicoleaceae].

The Temnomoideae are here defined as in Schuster (1967, pp. 68-69). The type of Temnoma, T. pulchellum (Hook.) Mitt. has a free shoot calyptra, a perianth developed to a moderate degree, the two arising from a distinct "coelocaul precursor"; cf. Schuster (1967, fig. 24:5). In T. palmatum (Lindb. ex Pears.) Schust., the perianth is more reduced and may not exceed the rather well-developed coelocaul in height (Schuster, 1967, fig. 44:1). It is only a small step to the condition in Leiomitra tomentosa (cf. Hatcher, 1959, fig. 1), and here one goes in an almost imperceptible gradation to the condition in L. lanata (Hook.) Schust., comb. n. [Basionym: Jungermannia lanata Hook., Musci Exot. 2: pl. 116, 1820], in which a low, caplike shoot calyptra and a very low perianth persist. And from there one can derive the perianth- and calyptra-free coelocaul of Trichocolea.

In effect, within Temnoma we find gradation almost to that in Leiomitra of the Trichocoleoideae. In Temnoma, the quadrifid leaf, often with the dorsal 1-2 lobes rather reduced, succubously inserted; the elongated-rectangular leaf cells with roughened cuticle; and the oil-bodies are identical to those in Trichocolea and Leiomitra. We also see opposed paired ciliation, with cilia of similar form (constituted of highly elongated cylindrical cells). The similarity in capsule-wall anatomy between Temnoma and Trichocolea was already commented on by Schuster (1959).

In essence, only two criteria seem to separate the Temnomoideae and Trichocoleoideae: the former has a tendency towards brownish wall pigmentation, the latter consistently lacks it; the former shows plastic branching, with retention (at least sparingly) of ventral-intercalary branches, the latter has evolved specialized, restricted branching modes, usually only Frullania type, with ventral-intercalary branches never present in any taxon I have seen. In view of the great diversity of branching modes from species to species within Temnoma (cf. Schuster, 1967), the last criterion loses significance perceptibly. I would conclude that Temnoma, in most respects, is midway between the other genera of Temnomoideae (in which paired-opposed ciliation never occurs, and in which a coelocaulle-precursor is unknown). The degree of coelocaulle elaboration in the Temnomoideae is highly variable: in Temnoma itself a coelocaulle-precursor seems always distinct: the foot of the sporophyte normally penetrates below the level of insertion of the  $\sigma$  bracts (Schuster, 1967, figs. 24:5, 44:1, 48:1), although in primitive species the perianth is better developed and the coelocaulle less elaborated (as in T. quadripartitum (Hook.) Mitt. and T. quadrifidum (Mitt.) Schust.; cf. Schuster, 1967, figs. 33:1, 30:5). In Archeochaete Schust., Lophochaete Schust., and Pseudolepicolea Fulf. & Tayl. the perianth is well developed and the coelocaulle virtually lacking or a mere precursor (cf. figs. 20:2, 14:4-5, in Schuster, 1967); in these taxa the foot appears never to penetrate below the level of insertion of the uppermost  $\sigma$  bract -- hence one cannot speak of a coelocaulle precursor with bracts inserted on it.

The subf. Blepharostomatoideae is first defined in Schuster (1967, p. 65); it is validly described (under Pseudolepicoleaceae) in Grolle (1972).

The subf. Chaetocoleoideae Schust., subf. n. is also first defined in Schuster (1967, p. 65), but a Latin diagnosis is outstanding. It follows (derived from Spruce, 1885): Foliis succubis, foliolisque palmatifidis, margine integerrimis; bracteis  $\sigma$  exterioribus ciliato-multifidis; perianthio abbreviato, ore longiciliato. Type (and only) genus. Chaetocolea Spr., Trans. Proc. Bot. Soc. Edinburgh 15:346, 1885.

## Family LEPIDOLAENACEAE

The intrageneric classification of this family remains controversial; with the transfer to it of Jubulopsis Schust., the perimeters of the family are visibly broadened. A needed segregate from Lepidolaena itself is the following:

Lepidogyna Schust., gen. n. Differt a Lepidolaena: (1) Coelocaula longissime claviforme; (2) paraphyllia in surculo primario vegetativo praesentia; (3) seta galearum basi bicellulariseriata; (4) capsula longissime elliptica-cylindrica. Type. Jungermannia menziesii Hook., Musci Exot., pl. 118, 1820 [= Lepidogyna menziesii (Hook.) Schust., comb. n.].

Also here is: Lepidolaena hodgsoniae Grolle, Jour. Hattori Bot. Lab. no. 30:29, 1967 = L. hodgsoniae (Grolle) Schust., comb. n.

Lepidolaena has a stoutly obpyriform coelocaula investing a short-ellipsoidal to ovoid capsule; the capsule wall is 3-4-stratose, with the strata of nearly equally thick cells, the inner with I- or U-shaped bands; the spores bear fine, spinulose, or coarse to fine papillae. In Lepidogyna the long-cylindrical coelocaula surrounds a cylindrical-ellipsoidal capsule; its wall is 6-7-layered; the high epidermal cells have evenly thickened radial walls, but inner cells are very delicate and lack distinct thickening bands; spores are covered with irregular, low, often furcate ridges and never bear papillae of any type. The ecology of the two genera is also drastically different.

Capsule-wall anatomy of Lepidogyna is closer to that of Neotrichocolea and Trichocoleopsis, which Inoue would place (on the basis of capsule-wall anatomy) into a family distinct from the Lepidolaenaceae. These and other facts may necessitate a reorientation of family limits; I think either the Jubulopsidoideae must be raised to family rank, or the Neotrichocoleaceae reduced to subfamily rank! A detailed generic revision of this family, with adequate illustrations, will be presented shortly.

## Family LEPIDOZIAEAE

Telaranea Spr. ex Schiffn.

Telaranea wallichiana (Gott.) Schust., comb. n. Basionym: Lepidozia wallichiana Gottsche, in G. L. & N., Syn. Hep., p. 204, 1845.

I have collected this east Asiatic taxon in Japan (1974); it is indubitably a member of Telaranea subg. Neolepidozia (Fulf. & Tayl.) Schust., as the symmetric leaves, leptodermous cells, and conspicuous hyaloderm demonstrate.

Lembidium Mitt.

I have shown (Schuster, 1963a) that of all the taxa referred to Lembidium, only L. nutans Mitt. can remain there; others go into Isolembidium Schust., Hygrolembidium Schust., Kurzia subg. Dendrolembidium (Herz.) Grolle, Megalembidium Schust., Chloranthelia



Schust., and Micropterygium Lindenb.! The sole extant species, L. nutans Mitt. is known only from New Zealand; from there, now, a second species can be recognized:

L. longifolium Schust., sp. n. Species L. nutanti cognata, distincta, autem, ut folia elongata, apices 4-lobuli, lobii angusti parvique caduci; cellulae basales foliorum satis amplificatae, non inflatae, cuticula papillosa sicut in reliqua lamina; ramificatio serialis frequens, typi Bazzaniae (typi Frullaniae semper ex eodem latere axis principalis lateraliter summoti enascens; ramificatio ita superficialiter furcata). Type. New Zealand. North Island: Mt. Hauturu, Little Barrier I., 1700-1900 feet (RMS 51443).

This species has a Bazzania-type disposition of the Frullania-type terminal branches: all branches issue only from one side of the leading axis. In L. nutans terminal branches are rare, solitary. Branching suggests that Lembidium s. str. is very different from Isolembidium Schust., Megalembidium Schust. (with Frullania- and Microlepidozia-type terminal branches), and Hygrolembidium Schust. (with only lateral + ventral-intercalary branching).

#### Family JUNGEMANNIACEAE s. lat.

Nothostrepta Schust., gen. n. Surculi apices Plagiochila-formes decurvatos habentes; folia biloba, margine posticali deflexo; gemmae nullae; amphigastria distincta; rhizoidea pauca, ad bases foliorum amphigastriorumque enascentia; ♂ bracteae in inflorescentia tenui spicata repertae, bracteis lobum anticalem inflexum habentibus; ♀ bracteae asymmetricae, profunde 2-3-fidae, lacinias et/aut lobos accessorios habentes; membrana capsulae 5-6-stratosa, cellulis epidermalibus altis (ca. 2X altioribus quam strata interna). Type. Plagiochila bifida Steph., Annal. Istit. Bot. Roma 2:86, 1886 [= Anastrophyllum bifidum (Steph.) Steph., Bih. Kgl. Sv. Vet.-Akad. Handl. 26(3):25, 1900] = Nothostrepta bifida (Steph.) Schust., comb. n.

Also falling here is, presumably (I have seen only sterile plants!), Nothostrepta longissima (Steph.) Schust., comb. n. [Basionym: Anastrophyllum longissimum Steph., Bih. Kgl. Sv. Vet.-Akad. Handl. 26(3):13, 1901].

Although these two species were placed into Anastrepta in two recent papers by Grolle, they diverge widely from that genus. Anastrepta, with a dorsally arched shoot apex, with gemmae, with dispersed rhizoids, is very distinct in numerous respects from Nothostrepta. The Plagiochila-like androecium is linked with a Jamesoniella-like gynoecium -- a most unusual combination. The decurved shoot tips of Nothostrepta are again found in these two genera (and in Cryptochila Schust.) -- but never in true Lophozioideae, to which I think Anastrepta belongs. A paper dealing with this problem will soon appear elsewhere.

## Family PLAGIOCHILACEAE

Plagiochilon Hatt.

A single species has been known from the Western Hemisphere. A second is now known from the Northern Andes, in Venezuela. The two differ as follows:

1. Leaves ovate, never incipiently bilobed, + imbricate, always opposite; all rhizoids on microphyllous stolons, in fascicles; trigones smaller, basal cells hardly trabeculate-thickened.

P. bryhnii (Steph.) Inoue

1. Leaves, in situ, appearing narrowly obovate (flattened, narrowly ovate-oblong to + lingulate), often incipiently bilobed (1 or 2 apical teeth enlarged); all rhizoids from bases of leafy branches, scattered; trigones coarse, nodose, in longer basal cells longitudinally confluent.

P. intermedium Schust., sp. n.

P. intermedium Schust., sp. n.

Species P. bryhnii ramificatione praevalide laterali-intercalari similis; differens, autem, ut (a) folia anguste oblonga, saepe primo biloba, atque orientatio foliorum remota necnon dispositio saepe alterna; (b) omnia rhizoidea ab axibus foliaceis enascentia, dispersa; (c) trigonae grossae, nodosae, in cellulis basalibus longioribus + confluentes. Type. Venezuela. Estado Merida: La Fria, 2500 m., above Merida, Sierra Nevada de Merida (RMS & L. Ruiz-Teran 76-1481c).

The species epithet indicates that this taxon is nearly intermediate between Plagiochila and Plagiochilon, suggesting that the earlier treatment of Plagiochilon as subg. Oppositae of Plagiochila is perhaps to be preferred.

Plagiochila Dumort.

P. fragmentata Schust., sp. n. Planta taxis sect. Bidentum similis foliis fractis et corpusculis oleosis homogeneis; distincta, autem, a omnibus his taxis, foliis confertis, postice secundis, obovato-bilobis, margine dorsali tubulariter revoluta et longe decurrente [basibus foliorum anticalibus iuxtapositis, duas lineas contiguas in superficie dorsali caulis effectis]; folia apicalia grosse dentato-lacerata. Type. Venezuela. Estado Merida: Sierra de Santo Domingo, ca. 3600 m., Paramo de Mucubaji (RMS & L. Ruiz-Teran 76-851d). Also found (usually in small quantity) in the Sierra Nevada de Merida (RMS 76-1460c) and Estado Tachira, S. of Villa Paez (RMS 76-2076a, 76-2077a). Although the strikingly fragmenting leaves and the (5)6-12(13) homogeneous oil-bodies suggest the Bidentes, specifically P. caduciloba and P. jamaicensis, these taxa are widely different in the short-decurrent and nontubular dorsal leaf margins; leaf form in this species is nearly unique.

## Family SCAPANIACEAE

Scapania subg. Scapaniella (Buch) Joerg.

S. calciphila Schust., sp. n. Gemmae 2-cellulares 9-12 x 14-18  $\mu$ ; cellulae marginales foliorum plerumque isodiametricae et cellulis intramarginalibus subaequae; cellulae grosse contiguae papillosae; lobus dorsalis parvus, per solum 0.2-0.35 distalem partem longitudinis discretus; carina 0.6-0.7 longitudinis lobi ventralis. Type. New Hampshire: Beaver Brook Falls near Colebrook, Coos Co. (RMS 74-2852a).

Unfortunately known from very few plants; this saxicolous and calciphilous plant seems allied only to S. vexata and S. glaucocephala (with which it agrees in size, color, and gemma form), differing in the cuticle covered with coarse, conspicuous, weltlike "papillae" and the oil-bodies, 2-4(5) per cell, as well as in the reduced dorsal leaf lobe.

## Family GYMNOTRIACEAE

Herzogobryum Grolle

Six species of this subantarctic genus are known; a seventh occurs in New Zealand:

H. filiforme Schust., sp. n. Species H. molli similis foliis paulum bilobis et colore pallide viridi; distincta, autem, ut cellulae parvae sine trigonis, 11-13 x 11-14  $\mu$  media folii in parte; distincta necnon ut surculi filiformes, solum ad 150  $\mu$  lat. necnon folia parva, solum 180-200  $\mu$  lat., minus quam 18 cellulis lat. Type. New Zealand. South Island: Mt. Cook Natl. Park, alpine tussock zone, above Sealy Lakes (RMS 67-4417).

The juvenile gynoecea bear recognizable perianths and no trace of any subtending Isotachis-type perigynium, hence this taxon must be referred to Herzogobryum rather than to Gymnotrium. Affinities are principally to H. molle (which is larger, with leaves 24-26 cells wide) and H. atrocapillum (which is piceous and has merely retuse to short-emarginate leaves).

## Family LEJEUNEACEAE

The Lejeuneaceae, especially of the Neotropics, continue to be a source of major difficulty. Intrinsically, the group is difficult: limited "architectural diversity" is linked with parallelism and convergence, to the point where generic and species perimeters are often obscured. Extrinsically, past work, especially that of Stephani, created a giant obstacle to real progress. In modern terms, extant diagnoses are useless. Generic placements, often in better than 50% of cases, are untenable. Hence, identification of "unknown" taxa is often virtually impossible -- aside from cases of stenotypic, taxonomically "simple" genera like Bryopteris and Acrolejeunea, for both of which we have recent revisions. No one has had the



courage to attack the real problematic genera, such as Lejeunea (with at least 12 estimated subgenera) and Cheilolejeunea (with 6 or more subgenera). As a result, one either places taxa of these genera into "limbo" or, if worked on at all, only a small percentage of collections can be named to extant species. Hence, it is almost unavoidable to create new species which eventually prove identical to "old" species hidden in the wrong genus or, often, wrong genera.

Study of old herbarium specimens, in most cases, leads one only a short distance on the road to taxonomic understanding. Branching patterns (and merophyte sequencing, especially on sexual branches) and oil-body criteria offer major clues to both evolution and taxonomy. They are virtually unknown for neotropical taxa.

Under these conditions, research based only on study of herbarium specimens is foredoomed to be the worst kind of "alpha taxonomy," useful only to clear away part of the logjam of accumulated, ill-founded names. Real understanding is possible only with a field knowledge of the species, allowing extrapolation from the environmental perimeters that, to a still-unappreciated degree, strikingly alter the phenotype of the species.

Despite these discouraging, limiting factors, the following taxa of Lejeuneaceae are described as novelties, in part because I cannot find earlier names (and assume they are new), but in part because, even though I assume we will eventually find earlier names (usually in the wrong genus), the taxa involved have been studied cytologically and the cytological data are desperately needed to work out the evolution and phylogeny of the family. The positive gain in establishing sound cytological data helpful in comprehending species-group, subgenus, and genus limits far exceeds the possible negative input from adding additional "unneeded" names.

#### Blepharolejeunea S. Arn.

This monotypic genus was described with inadequate detail by Arnell. My study of a type fragment revealed that a genus of Ptychanthoideae is at hand with only obscure affinities to other genera; a remote affinity to Lopholejeunea is possible. The affinity to the Ptychanthoideae became evident only after detailed anatomical investigation of Lejeunea (Brachio-Lejeunea) securifolia Spr. [Trans. Proc. Bot. Soc. Edinburgh 15:131, 1884], of which abundant living plants with sporophytes were studied in Venezuela, in 1976. This species bears no affinities to Brachiolejeunea (Spr.) Schiffn., but is allied to Blepharolejeunea. I question whether it is to be placed into Blepharolejeunea, a genus founded for plants unique in subfam. Ptychanthoideae in the strongly laciniate-dentate leaf lobes, or relegated to an adjacently posited genus. I once felt the distinctions were so striking that separate generic treatment was appropriate, but now think that segregation into an autonomous subgenus more correctly reflects current generic concepts; for this the following taxon is founded:

Blepharolejeunea subg. Oreolejeunea. Subgenus a subg. Blepharolejeunea differens ut (a) lobi foliorum bractearumque omnino edentati; (b) ♀ bractea suborbicularis, distaliter rotundata; (c) cellulae membranas solidas atque trigonas magnas et male definitas habentes. Type (and only) species. Blepharolejeunea securifolia (Spr.) Schust., comb. n. [for basionym citation see above].

The basically rectangulate leaf lobule, with sharp apical tooth, the "distalmost" tooth situated midway in the truncate sinus between keel and apical tooth, makes for a lobular structure very different from that in any true species of Brachiolejeunea. A detailed study of the genus is in progress, and a paper with three plates of pertinent drawings will soon appear.

### Lepidolejeunea Schust.

This genus, founded in Schuster (1963), has been regarded by some as merely a subgenus of Pycnolejeunea. A knowledge of the cytology of several taxa of both genera proves conclusively that they are very distinct in this respect. Indeed, Lepidolejeunea and Kingiolejeunea Robins. should be united; Pycnolejeunea subg. Perilejeunea Kachr. & Schust. also fits better here. Thus broadly defined, the genus consists entirely of taxa with scattered ocelli, whose size is identical to that of neighboring chlorophyllose cells; the chlorophyllose cells in all cases seen have either no oil-bodies or mere oil-droplets. Some taxa (L. dominicensis; cf. infra) bear caducous leaves; in the only Pycnolejeunea I have seen with asexual reproduction, the leaves show a curious fragmentation of the distal and anterior portions.

The following intrageneric classification, still provisional, seems to most nearly reflect what we know about the phylogeny of the genus.

Lepidolejeunea Schust., Nova Hedwigia, Beih. 9:139, 1963.

Subg. Lepidolejeunea Schust. Type. L. falcata (Herz.) Schust.

Subg. Perilejeunea (Kachr. & Schust.) Schust., comb. n.

Basionym. Pycnolejeunea subg. Perilejeunea Kachr. & Schust., Jour. Linn. Soc. Bot. 56:493, 1961. Type. Pycnolejeunea grandistipula G. ex Steph., Spec. Hep. 5:611, 1914 = Lepidolejeunea grandistipula (G. ex Steph.) Schust., comb. n.

Also probably falling here is Pycnolejeunea dentata Robins., The Bryol. 67:455, 1964 [= Perilejeunea dentata Robins., The Bryol. 70:55, 1967] = Lepidolejeunea dentata (Robins.) Schust., comb. n.

In addition, Lejeunea (Hygro-Lejeunea) devoluta Spr., Trans. Proc. Bot. Soc. Edinburgh 15:236, 1884 [= Lepidolejeunea devoluta (Spr.) Schust., comb. n.] falls here. Pycnolejeunea granatensis Steph., Spec. Hep. 5:610, 1914 [= Perilejeunea granatensis Robins., The Bryol. 70:55, 1967] appears identical.

Subg. Kingiolejeunea (Robins.) Schust., stat. n.

Basionym. Kingiolejeunea Robins., The Bryol. 70:53, 1967.

Type. Kingiolejeunea ornata Robins., The Bryol. 70:53, 1967 =

Lepidolejeunea ornata (Robins.) Schust., comb. n.

Subg. Lepidolejeunea appears to include a minimum of 6-9 species; the following, the only species of the genus I know which regularly bears caducous leaves, appears new:

Lepidolejeunea dominicensis Schust., sp. n. Species a omnibus aliis taxis Lepidolejeunea ut lobi foliorum libere caduci, lobulis persistentibus; gynoecea in ramis foliaceis + elongatis sita, ♀ bracteis bracteoleisque dentatis; innovationes gynoeceales typi Pycnolejeuneae, singulares. Type. Dominica: Freshwater Lake (RMS 66-609c).

I have collected a similar plant in Jamaica, probably referable to L. punctata, in which leaves are uniformly persistent and the thick-walled vegetative leaf cells lack oil-bodies entirely, or, rarely, bear a few almost imperceptible oil-droplets. In the Dominican plant leaf lobes (but not lobules) are freely caducous and the thin-walled chlorophyllose leaf cells bear 2-9 tiny oil-droplets of varying size (all under 1.2  $\mu$  in diam.).

The following new combinations, all in subg. Lepidolejeunea, are needed:

Lepidolejeunea borneensis (Steph.) Schust., comb. n. Basionym:

Hygrolejeunea borneensis Steph., Spec. Hep. 5:557, 1914.

Lepidolejeunea multiflora (Steph.) Schust., comb. n. Basionym:

Cheilolejeunea multiflora Steph., Hedwigia 34:243, 1895.

Lepidolejeunea bidentula (Steph.) Schust., comb. n. Basionym:

Pycnolejeunea bidentula Steph., Hedwigia 28:259, 1869.

Lepidolejeunea nicobarica (Steph.) Schust., comb. n. Basionym: P.

nicobarica Steph., Hedwigia 35:126, 1896.

Lepidolejeunea graeffei (Jack & Steph.) Schust., comb. n. Basionym:

Archilejeunea graeffei Jack & Steph., Bot. Centralbl. 60:104, 1894.

Lepidolejeunea integristipula (Jack & Steph.) Schust., comb. n.

Basionym: Pycnolejeunea integristipula Jack & Steph., Bot. Centralbl. 60:107, 1894.

### Echinocolea Schust.

This genus, originally monotypic (Schuster, 1963), soon had a second Bornean species assigned to it (Grolle, 1964). Field work in Dominica in 1966 made me aware of the fact that Trachylejeunea dilatata Evs. did not fit into that genus but belonged in Echinocolea. Also, Lejeunea prionocalyx G. fits only here. As a consequence, at least 4 species appear assignable to Echinocolea. A revision of the genus, with pertinent plates, will soon appear. Meanwhile, the following combinations are needed:

Echinocolea prionocalyx (G.) Schust., comb. n. [Basionym: Lejeunea prionocalyx G. in sched. = Trachylejeunea prionocalyx (G. ex Schiffn.) Schiffn., Engler's Bot. Jahrb. 23(5):592, 1897].

Echinocolea dilatata (Evs.) Schust., comb. n. [Basionym: Trachylejeunea dilatata Evs., Bull. Torrey Bot. Club 35:372, 1908].

The type of E. dilatata is from Jamaica. Plants I collected in Dominica appear to be subspecifically distinct:

Echinocolea dilatata subsp. antillana Schust., subsp. n. Subspecies a subsp. dilatata distincta ut ♂ et ♀ gametangia plerumque late seiuncta (plantae saepe velut dioeciae visae); ut cellulae marginales satis magnae (18-26  $\mu$ ) atque cellulae basales elongatae (2-3:1). Type. Dominica (RMS 67-505).

Oil-bodies in basal cells of these plants are (1)2-4(5) per cell, very large (to 7-8 x 12-24  $\mu$ ) and diagnostically granular, grayish and opaque or yellowish brown; they are smaller in median and distal cells. Oil-body characters are drastically distinct from those in Trachylejeunea s. str.

#### Trachylejeunea (Spr.) Schiffn.

The type of this genus, as well as that of subg. Hygrolejeuneopsis, has a lobule with two 1-celled teeth, nearly juxtaposed, between which the hyaline papilla is oriented. However, the type, T. acanthina, is unique in many respects (lack of subfloral innovations; lobes, underleaves, ♀ bracts and bracteoles spinose-dentate; cortical and medullary cells both leptodermous; cells nontuberculate; ocelli lacking). Subgenerically distinct are a series of species forming two autonomous subgenera, as follows:

Trachylejeunea subg. Hygrolejeuneopsis Schust., subg. n.

Subgenus a subg. Trachylejeunea distinctus ut innovationes subflorales plerumque singulares et sine innovationibus, interdum nullae; folium, amphigastrium, bractea et margines bracteolae edentata aut obscure denticulata; cellulae corticeae medullaresque pachydermatae; cellulae tuberculatae; ocelli adsunt. Type. Trachylejeunea aquarius (Spr.) Evs.

Trachylejeunea subg. Trachycoleus Schust., subg. n.

Subgenus a subg. Trachylejeunea distinctus ut lobulus unicum dentem habet, papillis hyalinis hoc manifeste proximalibus; gynoecea, saepe in axibus elongatis, 1(2) innovationibus subfloralibus praedita; innovationes variabiliter orientes, et taxilejeuneoideae et pycnolejeuneoideae, steriles aut denuo fertiles; lobi foliorum, amphigastria, bracteae et bracteolae omnes edentatae; cellulae non tuberculatae; ocelli basali adsunt. Type. Trachylejeunea monophthalma Schust. [cf. Schuster, Bull. Torrey Bot. Club 97:345, 1970]. T. grossepapulosa (Steph.) Schust. also fits here.

A paper dealing with the intrageneric classification and affinities of Trachylejeunea is in preparation; plates of the various

entities will be provided there.

Dactylophorella Schust., gen. n.

Plantae satis vigentes; caulis series cellularum 7 corticales + 5-8 medullares, habens, + leptodermatosus. Folia lobos ovato-triangulares habentia, pinnate lobulata, crispata, lobis secundariis spinoso-dentatis; lobus aspectu hispidus. Lobulus dente apicali 1-cellulari, obtuso, non-falcato praeditus. Ocelli nulli. Amphigastria lobos erectos quorum marginibus recurvatis, spinuloso-muricatis habentia. Type. Lejeunea muricata G. in G. L. & N., Syn. Hep., p. 348, 1845 [= Drepanolejeunea muricata (G.) Steph.] = Dactylophorella muricata (G.) Schust., comb. n.

A segregate from Drepanolejeunea, to which it is not at all closely allied. Differing from this in (a) lobulate dorsal lobes; (b) leptodermous stem cells, the medullary in 5-8 rows; (c) underleaves with erect, strongly spinulose lobes, the sinus U-shaped with reflexed margins; (d) apparent lack of ocelli. The merophyte sequencing is quite different, on the  $\phi$  branches, from that normal to Drepanolejeunea.

The presumed generic affinities will be dealt with separately, and a plate provided.

Cheilolejeunea (Spruce) Schiffn.

In Schuster (1980) the lectotype designation by Evans (1906), which is clearly and unambiguously based on that portion of the mixed original material that bears a spiniform 1-celled apical tooth, is accepted. This lectotypification was specifically emphasized in Evans; it was also accepted in Kachroo & Schuster (1961) and in Schuster (1955, 1963). The subgeneric division proposed in Schuster (1955, 1963) derives directly from the acceptance of Evans' original lectotypification. The later lectotypification by Grolle (1979), based on the fact that most numbers of Spruce's exsiccatae contain other taxa, in mixture or exclusively, is rejected for one simple reason: if we were to start relectotypification of all new taxa of Lejeuneaceae issued in more than one exsiccatus (one single packet), a Pandora's Box of mindboggling proportions would be opened and decades, if not centuries, would elapse while bryologists would try to study as many individual packets (isotypes) of all taxa issued by their predecessors. I refuse to play this "numbers game." Grolle seems unaware of one fact: in the Tropics almost all Lejeuneaceae occur in admixture, often 3-10 species or more within a single square foot on a tree trunk. Hence, many if not all early exsiccatae and most modern ones, unless they are systematically useless micro-collections, are badly mixed. Hence we have no rational alternative but to accept lectotypification by the first worker who revises a group, if that lectotypification is clear and rationally based. Spruce's set in Manchester, subsequent to Spruce's time regarded as the holotype, and the material examined by Evans (Y, NY), all con-



tain the plant with an aciculiform apical tooth of the lobule. Evans was the first to revise Cheilolejeunea sensu Spruce -- and to cleanse its limits (by, i.a., excluding Rectolejeunea, Leiolejeunea, and other elements). Having to choose between the initial Evans lectotypification -- which has stood unchallenged for nearly 75 years -- and the recent one of Grolle, I accept the first; there is nothing to be gained by accepting the latter except the need for perhaps creating at least one new subgeneric name and substituting subg. Cheilolejeunea for taxa now placed into subg. Euosmolejeunea.

Cheilolejeunea and Lejeunea are, by far, the most difficult genera of the entire family Lejeuneaceae. Taxonomic groupings in both genera that are based only on dead material can only be regarded as of temporary relevance: perhaps the single most relevant criterion in both genera are the oil-bodies, followed by ramification patterns. For understanding of both, abundant living plants are needed. Under these conditions, inevitably and unavoidably, the only rational way we may ever understand these genera is by re-describing the taxa from fresh material, basing our taxonomy on recently collected living plants and, with slowly accumulated comprehension of real species limits, to eventually, tentatively at least, place modern-based concepts and classical "species" into juxtaposition.

I know of no other group of Hepaticae for which the extant literature -- and especially that of Stephani -- forms a greater impediment to modern systematics. The conceptual bloc created is almost incredible. There are only two solutions: (1) to accept a herbarium-based and, by its nature, imperfect taxonomy that cannot even hope to qualify as "alpha taxonomy" -- using, as best we can, extant names; or (2) to start afresh and to base our systematics on the living organism, paying minimal attention to the dead fragments found in most herbaria. After decades of indecision, during which time I refrained from publishing new binomials for the simple reason that I could not, in any scientifically sound way, assure that the herbarium specimens of the 19th century were identical with sharply delimited taxonomic entities based on living plants, I have decided that the only sound scientific approach is to give the cytologically-based entities new names if I could not feel certain that the herbarium-based concepts were identical.

The following new taxa, from Jamaica, were studied from living plants in the 1960's; the names have been in MS since the plants were studied, microscopically, in Jamaica. After over a decade of indecision, it seems best to publish them -- even though, inevitably, there may be earlier names, probably in the wrong genus, that may eventually come to light.

Cheilolejeunea aciculifera Schust., sp. n. Plantae pallide virides, superficies loborum (apicibus loborum exceptis) asperae ob tubercula pachydermata, uno in omni cellula; cellulae marginales irregulariter denticulatae, tuberculis pachydermatis eminentibus armatae; carina basaliter levis, distaliter (ab ambitu visa)

denticulata; dens apicalis lobuli acuminatus, perelongatus, unicellularis; lobi foliorum obtusi, decurvati; lobi amphigastriorum saepe divergentes ut in Harpalejeunea, ad cacumina rotundati obtusive. Type. Jamaica: Trail to Caledonia Peak, Blue Mts. (RMS 67-025e); on fern frond.

Insofar as subg. Strepsilejeunea is distinct at all (I placed it, tentatively as subgenus, within Cheilolejeunea; cf. Schuster, 1963, p. 64, p. 112), this species fits that concept. Oil-bodies are coarsely botryoidal, occur (1)2-3 per cell, and measure 4-5 x 13 to 3.2-4 x 8-10  $\mu$ ; no trace of ocelli was seen. The keel has papilliform-elevated cells in its distal half only. The divergent and rounded to blunt-tipped underleaf lobes are distinctive. It is possible that this plant may prove identical to Trachylejeunea dominicensis Steph. (Spec. Hep. 5:303, 1915) but the lobule apex in that is described as ending in an "angulo obtuso."

Cheilolejeunea mammiifera Schust., sp. n. Planta pallida ad cinero-viridem; lobi acutissimi, apicibus decurvatis; dens apicalis lobuli tantummodo modicius longus, unicellularis; lobi ob tubercula pachydermata asperi, uno in omni cellula; carina atque superficies lobuli tuberculis grossis, fere sphericis armatae. Type. Jamaica: Caledonia Peak, 200-300 feet below summit; on Podocarpus bark (RMS 67-343).

The unisexual plants are known only from  $\sigma$  individuals; the sharp-pointed leaves bear a lobule with the 1-celled apical tooth only moderately elongated. Leaf cells are strongly armed with salient "tubercles" -- these are almost spherical on the lobule keel and surface and are so large they lie almost juxtaposed. The strongly armed leaves suggest Trachylejeunea, in which, however, the lobular papilla is proximal in orientation and monoecious inflorescences prevail. I have not seen the type of "Trachylejeunea" spruceana Steph. (Hedwigia 35:138, 1896). This is also dioecious and known only from  $\sigma$  plants but is very different in the rounded leaf lobes, not decurved at the apices -- and in the much less coarse armature of the leaves. "T." inflexa is similar, but monoecious.

#### New Combinations in Cheilolejeunea

Since about 1957 I have had, in manuscript, numerous recombinations under Cheilolejeunea of taxa formerly described in "genera" which I am convinced cannot be maintained as distinct from that genus. Included are taxa described under Euosmolejeunea, Strepsilejeunea, and Anomalolejeunea. I had once intended to prepare a world monograph of the group. However, experience with the North American-Antillean taxa has convinced me that no revision based largely on dead herbarium plants could possibly succeed. In the allied genus Leucolejeunea, my studies of thousands of individuals with regard to ramification patterns (cf. Schuster, 1980, where fragments of these studies are documented), branching modalities -- specifically gynoeceal orientations, the number and nature of subfloral innovations, if present -- have shown that wide variations

dependent on growth conditions of the population sampled prevail. The same is true in Cheilolejeunea, in which some taxa (e.g., C. rigidula; cf. Schuster, 1980) are immensely variable when growing under strongly disparate environmental stimuli. To my dismay, I found that the often fragmentary types (e.g., of C. myriantha), even when fertile, allow no taxonomically meaningful extrapolation. When sterile, the types are almost useless.

I would predict that any attempt to revise Cheilolejeunea s. lat., based only on use of herbarium material, will ultimately prove unsuccessful. I also realize that for workers unable to do the requisite field work, this is the only approach. Yet there is an air of futility about the endeavor: in the late twentieth century, only a nineteenth-century type revision is possible. Having thus come belatedly to this conclusion, I publish below certain new combinations, chiefly in order to place these taxa in their proper position. I have not seen types of many of these taxa and the specimens seen (chiefly from 1955-1963) may not prove authentic in a few cases; hence there is the possibility for erroneous conclusions. Also, realizing belatedly that taxonomic conclusions based on dead herbarium specimens are all suspect, I have not tried to evaluate these taxa; some, without doubt, will prove synonyms of earlier described species. However, in order to clean up generic perimeters, I place the species described below as follows:

Cheilolejeunea (Renilejeunea) montagnei (G.) Schust. (cf. Schuster, 1963, p. 64, p. 112). The winged keel of the ♀ bract is unique and, in spite of the lobular structure, this species may need to be excluded from Cheilolejeunea on this basis and on the basis of the unlobed underleaves.

Placing the species in Leucolejeunea would be no solution: in that genus the lobular hyaline papilla is situated on a projection in the sinus far removed from the "apical" tooth, whereas in C. montagnei the hyaline papilla is inserted on the distal base of the [1-celled] apical tooth, as in all other true Cheilolejeunea species I have seen. I have seen no type and wonder if the affinities of this plant are not closer to Aureolejeunea Schust. (1979).

Cheilolejeunea (Anomalolejeunea) pluriplicata (Pears.) Schust., comb. n. Basionym: Lejeunea (Anomalolejeunea) pluriplicata Pears., Christiania Vid. Selsk. Forh. 1:5, 1887 [= Anomalolejeunea pluriplicata Schiffn., Nat. Pflanzenfam. 1(3):127, 1893].

There is much confusion about this species; the figures in Vanden Berghen (1951, fig. 2) and Arnell (1963, fig. 134) suggest two taxa are at hand. Although Arnell describes (and fig. 134:b illustrates) the cells as with 2-3 botryoidal oil-bodies, his fig. 134 shows cells with solitary oil-bodies! His figures of lobular structure disagree wholly with those of Vanden Berghen.

Cheilolejeunea (Euosmolejeunea) robillardii (Steph.) Schust., comb. n. Basionym: Euosmolejeunea robillardii Steph., Spec. Hep. 5:578, 1914.

Cheilolejeunea (Euosmolejeunea) brachytoma (G.) Schust., comb. n.  
Basionym: Lejeunea brachytoma G., Abh. Nat. Ver. Bremen 7:355, 1882.

Cheilolejeunea (Euosmolejeunea) grandistipula (Steph.) Schust., comb. n.  
Basionym: Lejeunea grandistipula Schiffn., Engler's Bot. Jahrb. 8:89, 1887 [= Euosmolejeunea grandistipula Steph., Spec. Hep. 5: 576, 1914].

Cheilolejeunea (Euosmolejeunea) longiflora (Tayl.) Schust., comb. n.  
Basionym: Lejeunea longiflora Tayl., Lond. Journ. Bot. 5:396, 1846.

Cheilolejeunea (Euosmolejeunea) coronalis (G.) Schust., comb. n.  
Basionym: Lejeunea coronalis G., in G. L. & N., Syn. Hep., p. 361, 1845.

Cheilolejeunea (Euosmolejeunea) fragrantissima (Spr.) Schust., comb. n.  
Basionym: Lejeunea (Euosmo-Lejeunea) fragrantissima Spr., Trans. Proc. Bot. Soc. Edinburgh 15:243, 1844.

Cheilolejeunea (Euosmolejeunea) laxiuscula (Spr.) Schust., comb. n.  
Basionym: Lejeunea (Euosmo-Lejeunea) laxiuscula Spr., Trans. Proc. Bot. Soc. Edinburgh 15: 244, 1844.

Cheilolejeunea (Euosmolejeunea) suaveolens (Spr.) Schust., comb. n.  
Basionym: Lejeunea (Euosmo-Lejeunea) suaveolens Spr., Trans. Proc. Bot. Soc. Edinburgh 15:245, 1844.

Cheilolejeunea (Euosmolejeunea) subcrenulata (Spr.) Schust., comb. n.  
Basionym: Lejeunea (Euosmo-Lejeunea) subcrenulata Spr., Trans. Proc. Bot. Soc. Edinburgh 15:245, 1844.

Cheilolejeunea (Euosmolejeunea) comans (Spr.) Schust., comb. n.  
Basionym: Lejeunea (Euosmo?-Lejeunea) comans Spr., Trans. Proc. Bot. Soc. Edinburgh 15:246, 1844.

Cheilolejeunea (Strepsilejeunea) krakakammae (Lindenb.) Schust. (1963, p. 112).  
Basionym: Lejeunea krakakammae Lindenb., in G. L. & N., Syn. Hep., p. 353, 1845 [= Strepsilejeunea krakakammae Steph., Hedwigia 29:74, 1890].

Cheilolejeunea (Strepsilejeunea) brevifissa (G.) Schust., comb. n.  
Basionym: Lejeunea brevifissa G., Abh. Nat. Ver. Bremen 7:356, 1882.

Cheilolejeunea (Strepsilejeunea) georgiensis (S. Arn.) Schust., comb. n.  
Basionym: Strepsilejeunea georgiensis S. Arn., Bot. Not. 1953:179, 1953.

Lejeunea Libert

With at least 11-12 groupings that are best regarded as subgenera, Lejeunea may prove to be the largest genus of the family. It is also the most difficult (cf. Schuster, 1963, p. 128 et seq.; Schuster, 1980). Not only is the intrinsic difficulty enormous--several other sources of possible error must be considered: (a) A very large ensemble of "species" -- a veritable floating poulation -- of unstudied taxa exists, described under "Lejeunea"; most, but not all, belong to other genera. (b) As in Cheilolejeunea, oil-body types + ramification patterns offer two of the most important criteria for species and group discrimination; as in Cheilolejeunea, androecial form ( $\sigma$  bracteoles only at base;  $\sigma$  bracteoles throughout androecium) is equally important. Oil-bodies are known for few species; ramification patterns cannot be adequately deduced from most of the scrappy type material seen -- and the patterns, sufficiently malleable intrinsically, are furthermore subject to manifest changes with environmental differences; androecia are inadequately described in almost all extant diagnoses, most of which, in general, are useless in any modern sense. Under these conditions, descriptions of new taxa seem almost futile; yet the following three, after much search, could not be placed.

Lejeunea (Lejeunea) cyanomontana Schust., sp. n. Gynoecia, saltem partim, acrogyna, numquam  $\sigma$  innovationibus praedita; cellulae pauca corpuscula oleosa segmenta habentes; lobuli longi (ad 0.5 longitudinis lobi) dente apicali + hamato praediti; caulis 7-9 series cellularum medularium habens. Type. Jamaica: Caledonia Peak, Blue Mts. (RMS 67-345a).

This small species (sterile axes only 450-520  $\mu$  wide) may be sought under subg. Microlejeunea; the stem, however, has 7-9 rows of medullary cells. In this, in the autoecious inflorescences, the obliquely ascending leaves, and abbreviated union of bracts + bracteoles in the gynoecium, as well as in aspect, it is similar to L. autoica Schust. At once distinct in the larger underleaves, 140-160  $\mu$  broad, with lobes 5-6 cells wide, contiguous and rather elevated leaves, more compact androecia, lobes and lobule apices of  $\phi$  bracts normally broadly rounded.

Lejeunea (Lejeunea) androgyna Schust., sp. n. Gynoecia omnia in ramis lateralibus brevibus sita, innovatione 0 vel  $\sigma$ , longitudine determinatis; cellulae pauca corpuscula oleosa segmentata habentes; dens apicalis lobularis obtusus, non hamatus; cellulae corticeae ventrales parvae, ca. 25  $\mu$  lat. Type. Jamaica: Caledonia Peak, Blue Mts. (RMS 67-345b).

Gynoecia in this plant are, almost without exception, on very short lateral branches, each of which often produces a small, spicate, often curved androecial innovation, or, alternatively, are innovation-free; no gynoecia with sterile innovations have been



seen. The segmented-botryoidal oil-bodies and aspect otherwise suggest L. glaucescens G., an otherwise exceedingly distinct species. I have seen a single athenal, infra-axillary, Radula-type, sterile branch in this species; this occurs again, in known taxa, only in plants currently referred to Taxilejeunea s. amplo (cf. Schuster, 1980).

Lejeunea (Microlejeunea) capillaris subsp. antillana Schust., subsp. n. Subspecies a subsp. capillari different ut dens apicalis lobuli plene expositus; amphigastria maiora, 120 x 85  $\mu$ ; lobi maiores 250 x 150  $\mu$ . Type. Jamaica: Caledonia Peak, Blue Mts. (RMS 67-341a).

Distinct from L. capillaris G. s. str. in the orbicular underleaves, the  $\phi$  bracts with lobuli much shorter than the lobes, and in other criteria. Perhaps an autonomous species.

Cololejeunea (Spr.) Schiffn. and Aphanolejeunea Evs.

Plants of these two genera, especially when epiphyllous, often occur in very small populations, and often badly mixed [I have seen as many as 8-9 species on a single leaf!]. Lectotypifications here need to be practiced with wisdom and restraint, in order to avoid creation of enormous chaos. I am aware of many problems because of mixed collections; I trust that an eventual monographer will exercise the requisite restraint.

Although often regarded as identical (most recently by Stotler & Crandall-Stotler, 1977), the two genera are very distinct, even at first glance, by their branching modes alone (Schuster, 1980).

Speciation has been almost as explosive here as in Lejeunea. The very small size and occurrence often as only isolated plants make study of the smaller taxa (and of all Aphanolejeunea) difficult. Many undescribed taxa remain, and species limits are often imprecise. The following five taxa, all from Jamaica, appear to be undescribed.

Cololejeunea papulosa Schust., sp. n. Species ab omnibus taxis Americanis distincta ut cellulae lobulorum perelongatae atque saepe sigmoideae; cellulae carinae inflatae papulosaeque; perianthium dorsaliter complanatum; folia anguste ovata. Type. Jamaica: Trail from Hardwar Gap to Caledonia Peak, Blue Mts. (RMS 67-025a).

Similar to Aphanolejeunea diaphana in the narrowly ovate leaves, widest below the middle, and in the 2-celled tooth of the lobule apex. Leaves, however, are not dimorphic; gemmae occur on ventral lobe faces; cells are nontuberculate; the keel is margined by strikingly papulose-inflated cells, while the lobule itself is formed of narrow, elongate, often sigmoidal cells.

Cololejeunea parallelifolia Schust., sp. n. Folia lingulata, ad apicem rotundata; perianthium non complanatum, carinis supra + angulatis denticulatisque; gemmae 16-cellulares, angulares; cellu-

lae foliorum inflatae, numquam tuberculata; planta paroecia.

Type. Jamaica: Trail from Hardwar Gap to Caledonia Peak, Blue Mts. (RMS 67-025).

Constantly paroecious; even  $\sigma$  bracts may bear antheridia. Lobular structure (lobule ending in a 2-celled tooth) as in the foregoing and as in A. diaphana. Distinct in the nondimorphic leaves, rounded leaf lobes, often rather obovate-oblong, and the nonpapulose cells of the leaf keel.

Aphanolejeunea lancifera Schust., sp. n. Dens apicalis lobularis 2-cellularis; hamatus, folia semper valde dimorphica; folia lobulata lobulos 0.5-0.6 longitudinis loborum habentia; lobi lanceolati, longitudo:latitudo 3-4:1; carinae perianthii natura leves.

Type. Jamaica: Below summit of Caledonia Peak, Blue Mts. (RMS 67-342).

Distinct from the A. gracilis-verrucosa-ephemeroides complex in the 2-celled apical lobular tooth which is optimally developed, strongly hooked, almost impinging on the keel apex. Perhaps allied to A. cingens Herz. but the latter differs in being smaller (leaves 260  $\mu$  long vs. to 325  $\mu$  long), has wholly smooth leaf cells (in A. lancifera the keel, distally, has strongly tuberculate cells), and bears elobulate leaves only 3-4 cells long (4-6 cells wide x 5-8 cells long in A. lancifera).

Aphanolejeunea gracilis var. linearifolia Schust., var. n. Varietas a var. gracili differens ut omnia folia linearis, elobulata;  $\sigma$  bracteeae  $\pm$  lineari-lanceolatae; cellulae perianthii carinarum et inter carinas forma tuberculorum obtusorum elevatae.

Type. Jamaica: Trail from Hardwar Gap to Caledonia Peak, Blue Mts. (RMS 67-025).

The remote, almost uniformly elobulate leaves are only 2 cells wide and consist of ca. 7-8 elongated "cell tiers" -- formed, except at the tip, of 2 cells, side-by-side; each leaf is terminated by a single sharp cell. Occasional plants produce an isolated lobulate leaf, with the 2-celled apical tooth of typical A. gracilis. Perianths are bluntly tuberculate on both keels and the intervals between them, unlike in A. gracilis proper. The latter, although described as dioecious, is, like the var. linearifolia, unquestionably autoecious.

Aphanolejeunea jamaicensis Schust., sp. n. Dens lobularis apicalis unicellularis; folia hispid-tuberculata, tuberculis altis, ad cacumina incrassata; lobi foliorum 2-2.2 plo longiores quam lati, cacuminibus plerumque in 2 cellulas terminantibus; folia elobulata minora quam lobulata. Type. Jamaica: Track from Hardwar Gap to Caledonia Peak, near waterfall, Blue Mts. (RMS 67-019).

The autoecious species is close to A. sicaefolia in the 1-celled apical lobular tooth. However, the type is mixed with the

latter and clearly distinct in: the tuberculate, hispid cells (never hispid in admixed A. sicaefolia) present throughout except for lobular surface; lobes ending in (1)2 single cells; elobulate leaves ca. 150  $\mu$  long and much smaller than lobulate ones;  $\sigma$  bracts with lobules ca. 5-7-celled.

#### Family JUBULACEAE

Asakawa et al (1979, p. 73) recently split this family into two, Jubulaceae and Frullaniaceae. Among the primary criteria cited for this segregation is seta anatomy: Jubulaceae with a 16 + 4-seriate seta, Frullaniaceae with it "composed of many, irregularly arranged cell rows." On that basis Amphijubula Schust. (Schuster, 1970) would have to be placed into the Jubulaceae, even though its other criteria (spores large, with rosette-type tubercles on surface; subfloral innovation, when present, Frullania type; copper-colored cell walls; Frullania-type  $\sigma$  branches, the androecium with a bracteole at base only) clearly assign it to a position nearer to Frullania. Engel (1978) had, indeed, placed Amphijubula under Frullania. I think the positions of both Asakawa et al. (1979) and Engel (1978) are untenable. They illustrate perfectly my statement (Schuster, 1970) to the effect that once the initially bigeneric Jubulaceae are studied more carefully, the taxonomy of the family would become "much more complex" -- and that "before it becomes simpler it will become more complex still." In the light of these two recent papers, which are conceptually poles apart, my predictions acquire an aura of prescience.

Ultimately, I think a taxonomic position somewhere between the two recent extremes adopted will prove most generally acceptable; such an intermediate position will necessitate the adoption of Amphijubula as a genus, and will entail the following new combinations:

Amphijubula Schust., Jour. Hattori Bot. Lab. 33:301, 1970.

A. microcaulis (Gola) Schust., comb. n. Basionym: Frullania microcaulis Gola, Nuovo Giorn. Bot. Ital. II, 29:172, 1923.

Synonym: Amphijubula spruceana Schust., Jour. Hattori Bot. Lab. no. 33:301, 1970.

Gola described his plant as dioecious; this error misled me into thinking that the clearly monoecious A. spruceana was distinct.

A. lobulata (Hook.) Schust., comb. n. Basionym: Jungermannia lobulata Hook., Musci Exot. 2: pl. 119, 1820 [= Frullania lobulata Dumort., Rec. d'Obs., p. 13, 1835].

Engel states that this plant finds its "closest relative" in A. microcaulis and I therefore transfer it to that genus. Since I have not seen sporophyte-bearing material, an element of uncertainty remains as to its proper generic provenance.

## FOOTNOTE

1

Professor of Botany, University of Massachusetts, Amherst.  
I am indebted to Dr. Hannah Croasdale for the Latin diagnoses.

## LITERATURE CITED

- Arnell, S. 1963. Hepaticae of South Africa. Pp. 1-411, figs. 1-290. Stockholm.
- Asakawa, Y., N. Tokunaga, M. Toyota, T. Takemoto, S. Hattori, M. Mizutani & C. Suire. 1979. Chemosystematics of Bryophytes II. The distribution of Terpenes in Hepaticae and Anthocerotae. Jour. Hattori Bot. Lab. no. 46:67-76.
- Engel, J. J. 1978. A taxonomic and phytogeographical study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. Fieldiana 41:i-viii, 1-319.
- Evans, A. W. 1906. Hepaticae of Puerto Rico. 6. Cheilolejeunea, Rectolejeunea, Cystolejeunea and Pycnolejeunea. Bull. Torrey Bot. Club. 33:1-25, pls. 1-3.
- Fulford, M. 1962. Manual of the leafy Hepaticae of Latin America. Part I. Mem. N.Y. Bot. Gard. 11(1):1-172 [publ. 1963].
- Grolle, R. 1964. Eine neue Echinocolea auf Celebes. Bot. Mag. Tokyo 77:333-335.
- \_\_\_\_\_. 1972. Die Namen der Familien und Unterfamilien der Lebermoose (Hepaticopsida). Jour. Bryol. 7(2):201-236.
- \_\_\_\_\_. 1979. Miscellanea hepaticologica 171-180. Jour. Bryol. 10(3):263-272.
- Hatcher, R. E. 1959. The structure of the female inflorescence and its taxonomic value in the genus Trichocolea. Lloydia 22(3):208-214, figs. 1-6.
- Inoue, H. 1976. Illustrations of Japanese Hepaticae. 2:1-194. Tokyo.
- Kachroo, P. & R. M. Schuster. 1961. The genus Pycnolejeunea and its affinities.... Jour. Linn. Soc. Bot. 56(368):475-511, figs. 1-16.
- Schuster, R. M. 1955. North American Lejeuneaceae I. Introduction; keys to subfamilies and genera. Jour. Elisha Mitchell Sci. Soc. 71(1):106-126.
- \_\_\_\_\_. 1959. Studies on Hepaticae. I. Temnoma. Bryologist 62:233-242.
- \_\_\_\_\_. 1963. An annotated synopsis of the genera and subgenera of Lejeuneaceae. I. Nova Hedwigia, Beih. 9:1-203.
- \_\_\_\_\_. 1963a. Studies on Antipodal Hepaticae. I. Annotated keys to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. Jour. Hattori Bot. Lab. no. 26:185-309.

- Schuster, R. M. 1966. The Hepaticae and Anthocerotae of North America. Pp. i-xvii, 1-802, figs. 1-84. Columbia University Press, New York.
- 1967. A memoir on the family Blepharostomataceae. *Candollea* 21(1):59-136, figs. 1-21. *Ibid.*, part II. *Candollea* 21(2): 241-355, figs. 22-50.
- 1970. Studies on Antipodal Hepaticae, III. Jubulopsis Schuster, Neohattoria Kamimura and Amphijubula Schuster. Jour. Hattori Bot. Lab. no. 33:266-304, figs. 1-6.
- 1979. Studies on Venezuelan Hepaticae, II. *Phytologia* 39(6): 425-432.
- Spruce, R. 1884-85. Hepaticae amazonicae et andinae. (Hepaticae of the Amazon and of the Andes of Peru and Ecuador). Trans. Proc. Bot. Soc. Edinburgh 15:i-xi, 1-590, pls. 1-20.
- Stotler, R. E. & B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. *Bryologist* 80: 405-428.
- Vanden Berghen, C. 1951. Note sur quelques hépatiques récoltées par R. E. et T. Fries en 1922, au Mont Kénia. *Sv. Bot. Tidskr.* 45(2):362-367, figs. 1-3.